

**Nest Site Selection in *Forpus passerinus* (Green-rumped Parrotlet)****Timothy C. Bonebrake**

**Abstract** How fitness is influenced by habitat features within a landscape underlies source-sink concepts and is important to population dynamics and conservation. I relate productivity to habitat quality measured at microhabitat and neighborhood scales in a box-nesting population of *Forpus passerinus* (Green-rumped parrotlets) in Venezuela. At 106 nest boxes I measured vegetation cover, vegetative structure, water depth, water cover, and food availability and related them to measures of productivity (young fledged per year and young fledged per year used) and their components (annual number of young produced per nest, nesting attempts, probability of successful nest, and number of years used). Principal component analyses resulted in three factors indicating high canopy cover and ground cover, high vegetation counts from the ground to 2 meters, and high water cover and greater water depth respectively at both the microhabitat and neighborhood scales. Linear regression models of these factors on the measures of breeding productivity show that nests in more open neighborhood habitat with less vegetative cover produced greater numbers of fledglings than did boxes with more cover where more predation occurs. Also, boxes associated with greater water depths had lower predation rates. A habitat manipulation experiment showed that boxes more in the open had a higher survival rate and that predation may be the major cause in the formation of the observed patterns.

**Introduction**

One of the crucial questions in any conservation problem is what are the factors that facilitate reproductive success or failure (Caughley 1994)? Reproduction influences the form of the ecology and evolution of a species and must be understood in order to develop any serious conservation program. Examination of the patterns and processes that drive reproduction in birds can aid in their conservation and provide for a more complete understanding of their life histories and population dynamics.

Differences in reproductive success among nest sites in birds has been attributed to variation in abiotic factors, such as microclimate (Holway 1991, Walsberg and Schmidt 1992, With and Webb 1993, Martin 2001), and in biotic factors, such as predation (Collias and Collias 1984, Martin and Roper 1988, Kelly 1993, Martin 1993, Martin 1995), intraspecific competition (Brooke 1979), intraspecific cooperation (Arnold 2000, Siepielski et al. 2001), and interspecific competition (Cody 1985, Martin and Martin 2001). The habitat features that may cause this variation in nest site quality provide the interface for which competition, predation, cooperation, and climate operate (Martin 1992). Habitat use patterns in birds are therefore important to conservation (Lawler and Edwards 2002, Winter et al. 2004) but the processes that create these differences are poorly known (Clark and Shutler 1999).

Predation is the primary cause of nest failure in most birds (Ricklefs 1969) and could be the major evolutionary force in determining nest site selection (Martin 1995, 1998). Many birds select nest sites in dense vegetation to conceal the nest from predators (Collias and Collias 1984). Nest sites concealed in denser foliage are often associated with lower predation (Martin 1988, Martin and Roper 1988). Other studies, however, have shown no evidence of this due to conflicting results from a complex and differentiated set of nest predators (Holway 1991, Filliater et al. 1994, Hanski et al. 1996). Furthermore, grassland species can experience greater nest predation rates if they nest closer to more structurally complex woodland environments where more predators occur (Wilcove 1985, Winter et al. 2000).

Scale is another important aspect of nest site quality. Determinants of nesting success can potentially operate at the landscape (~100 meters or greater) (Luck 2002, Tarvin and Garvin 2002), neighborhood (~10 meters or smaller) (Martin 1998, Rangen et al. 1999,

Chase 2002, Mezquida and Marone 2002), and microhabitat (characteristics of a given nest within its nest patch, e.g. nest height) scale (Kelly 1993). Each of these scales could exhibit different selective forces and result in distinct patterns (Kelly 1993).

With so many populations of New World parrots on the decline (Beissinger and Snyder 1992, Bennett and Owens 1997), it is crucial to understand the environmental factors and processes that facilitate success. The relationships between the breeding productivity of parrots and their habitat found in previous studies have been useful in conservation (Lanning and Shiflett 1983, Renton and Salinas-Melgoza 1999). *Forpus passerinus* (green-rumped parrotlet) is ideal for studying these relationships because for over 15 years every nest has been documented (Stoleson and Beissinger 2001). Parrotlets are also of interest because their range has been expanding into human disturbed environments (Hilty 2003). Being an abundant and successful species allowed experimental manipulations without detriment to the survival of that species.

In this study we examined how breeding success in *F. passerinus* varies among nest sites across a landscape. Multiple scales were used to examine variation between habitat and breeding success. To more fully understand the processes creating these patterns, we also examined differences in predation and other causes of nestling mortality within the population. Finally, a habitat manipulation experiment was conducted to see how breeding success differed in the context of habitat change.

## Methods

**Study Site and Species** Data collection took place at the Hato Masaguaral (8°34' N, 67°35' W), a ranch in the Venezuelan Llanos- a seasonal savanna with distinct wet and dry periodicity. The seasonal variation, with dry seasons receiving little or no rain and wet seasons averaging between 1000 and 2000 mm/year, along with its drainage capabilities dictates the form of this grassland (Beard 1955). On the ranch, the physiographic savanna units (as defined by Troth 1979) of relevance to this study are the sandhills (medano), the moderately flooded savanna (bajío), and the deeply flooded savanna (estero). The sandhills and deeply flooded savanna are characterized by scattered trees while the moderately flooded savanna can range from scattered trees to shrub-woodland cover up to 100% (Troth 1979).

In 1988 106 nest boxes made of polyvinyl chloride (Beissinger and Bucher 1992) were set up in 1989 for a population of *Forpus passerinus* (green-rumped parrotlet) and on at least every third day between 1988 and 2004, nest checks of the boxes have taken place during the breeding season (May to December). Nest checks consist of a.) counting, marking, and weighing eggs (see Waltman and Beissinger 1992) and b.) identifying individual nestlings and parents through the use of colored metal bands (Sandercock and Beissinger 2002).

*F. passerinus* is a small (24-36 g) sexually dimorphic parrot that feeds primarily on grasses and forbs, including *Croton hirtus* and *Hyptis suaveolens* (Waltman and Beissinger 1992). Breeding occurs exclusively during the wet season and nesting takes place in available cavities; generally nest boxes, tree holes, or fence posts (Beissinger and Bucher 1992). The strong intraspecific and interspecific competition for nest boxes suggests that this population is limited by nest site availability (Beissinger and Waltman 1991, Waltman and Beissinger 1992).

**Productivity Components** I examined breeding productivity by nest box. I used data collected from 1994 to 2003 because these years had little experimental manipulation to confound productivity analyses. Each box was given a value for each of the following components: young fledged per year, young fledged per year used, nesting attempts, probability of successful nest, fledglings per successful nest, average clutch size, first egg date (standardized by year to eliminate annual variation), and number of years used. The relationships between these components were explored. Nesting mortality was also examined by using the same dataset and calculating rates of predation and conspecific nest mortality.

Though the scale of the nest box was the primary scale for breeding productivity, I also examined productivity at two other scales, the fence and area scale. Each nest box is on a fence line and to obtain values for any given fence line, the mean productivity component values of the boxes within that fence line were calculated. Distinction of one fence line from another was qualitatively determined by approximate location and physiographic features. Each fence line was then classified under one of two areas; upland and lowland (fig. 1). Forty nest boxes are located within the lowland (5 fence lines) and 66 nest boxes are located within the upland (10 fence lines). The lowland is

distinguished by a more prominent shrub and woodland cover and more water (moderately flooded savanna) while the upland contains mostly open pasture (sandhills). Analyses were often done separately between the two areas based on evidence that these two areas contain distinct metapopulations of *F. passerinus* and exhibit independent population dynamics.

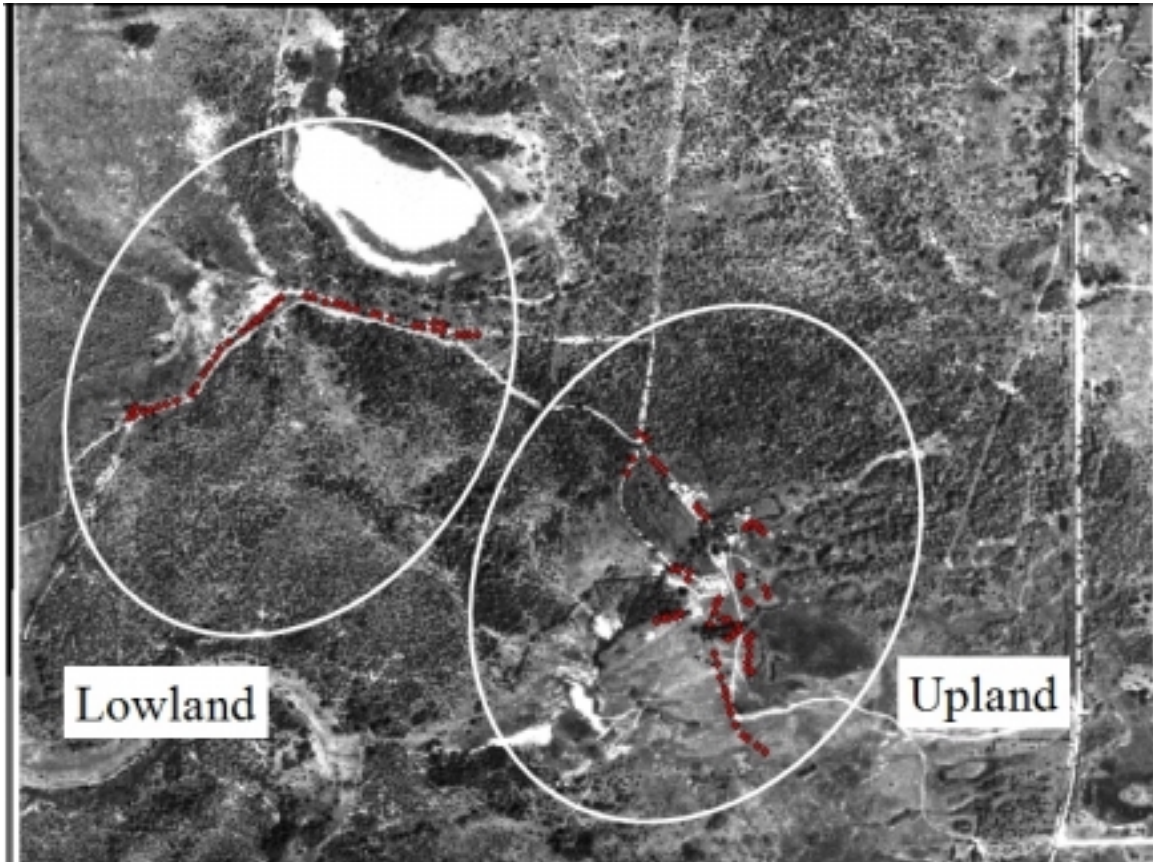


Figure 1. An aerial view of the study site used to analyze large scale habitat features. Note the differences between the lowland and upland habitat.

**Habitat Characterization** For the smaller scale habitat analysis, intensive field sampling was required. Neighborhood in this analysis is defined by a radius of ten meters around the box. Ten meters was chosen as a descriptor of neighborhood because the nest boxes were approximately 20 meters apart from one another meaning that once past a radius of ten meters, habitat variables became less distinct from one another and began repeating themselves between the nest boxes. Also, past studies have used ten meters as a reasonable radius for neighborhood size (see for example Chase 2002). Spatial correlation may overestimate the results of this analysis but I believe that the

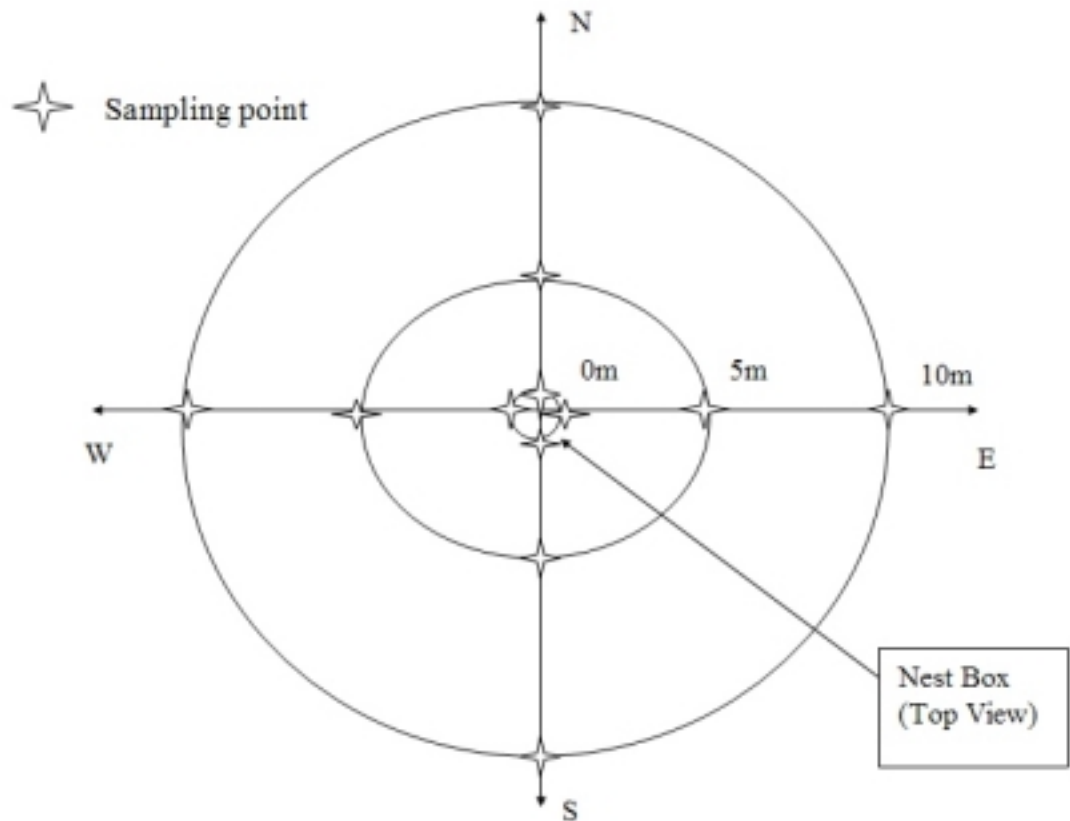
variation in habitat from one box to another is independent and that spatial correlation will not substantially affect the results. Microhabitat describes the specific nesting site, or the 0 meter sampling points. Because all nest boxes are at equal height and have equal dimension these variables were not included in the analysis.

One variable, likely of importance to parrotlet nestling viability, is vegetation cover. There is both a vertical and a horizontal component to vegetation cover and this was estimated by standing a pole into the vegetation. By placing a pole within the grasses, forbs, and shrubs around each nest site, an estimate of vertical cover was established by simply marking where each plant strikes the pole and measuring the markings. Horizontal cover with respect to each nesting site was determined by a small grid (0.085 m by 0.085 m) with 100 quads placed on the ground and quads with vegetation counted. Canopy cover was calculated the same way by holding the grid straight up, arms extended and counting quads. The pole and grid were placed in the ground and corresponding vegetation was measured 12 times; at 0, 5, and 10 meters, in each direction (fig. 2). Forage abundance was calculated by placing a 0.75 meter diameter hoop and counting individuals of *Croton* and *Hyptis* species (known food sources) within that hoop at each of the sampling points. Other factors around the nesting site, such as water, were also noted and analyzed by measuring the depth and noting the percent water cover with the grid (0.085 m by 0.085 m) at each of the 12 sampling points.

This sampling provides something of a snapshot of the habitat at the nest box because sampling only took place at a given nest box once. The field site is a ranch where mowing and tree trimming are common practices. Therefore, from one day to the next, significant changes to the nest box sites were possible. Also, the habitat data was taken all in the summer of 2004 while the productivity data was collected from 1994 to 2003, requiring the assumption that the nest box habitats don't change in a relative manner from one year to the next.

This habitat data (canopy cover, ground cover, water cover, water depth, *Croton* stems, *Croton* pods, Non-*Croton* stems, vegetation counts from 0 to 0.5, 0.5 to 1, 1 to 1.5, and 1.5 to 2 meters) was then analyzed by means of a principal component analysis (PCA) in order to find related variables and reduce the number of variables used in the analysis. The habitat factors as described by the PCA were analyzed with the

productivity factors produced from data from years past. Linear regression between the productivity variables and the habitat factors were done using Systat Version 10.0.



**Figure 2.** Sampling design for neighborhood (all sampling points) and microhabitat (sampling points taken at 0 m).

**Habitat Manipulation** A subset of infrequently used boxes ( $n=22$ ) were chosen for an experimental manipulation. The “infrequently” criteria used was that no more than two nests had been attempted within the past five years. Considering that often boxes are used three times a year, two nests or less out of five years is quite small. Of these, pairs were chosen based on spatial proximity to one another and an experimental or control status was assigned randomly to each box within that pair. The control box was left unmanipulated while the vegetation at the experimental box was leveled within a ten meter radius by means of a machete. The birds were then able to nest in all boxes and differences between control and experimental boxes were explored.

## Results

**Variation in Productivity among Boxes, Fences, and Areas** Breeding success varied greatly among the boxes (Table 1). Boxes varied from fledging no nestlings per year to over eight fledglings per year. Boxes were used a minimum of 3 years and a maximum of 10 years. The average probability of producing a successful nest was 0.48 and ranged from 0 to 0.93. The number of young produced per successful nest varied little among boxes.

Table 1. Summary statistics and relationships between components of *Forpus passerinus* breeding productivity from 1994-2003.

Productivity Components	$\bar{x} \pm SE$	Range	<i>Correlation Coefficient (r)</i>				
			Nesting Attempts	Fledged/ Succ. Nest	Prob. of Succ. Nest	Years Used	Fledged/ Year Used
<i>Nesting Attempts</i>	11.8 ± 0.5	3-26	-	-	-	-	-
<i>Fledged/ Succ. Nest</i>	4.5 ± 0.0	2.57-6.25	0.03	-	-	-	-
<i>Prob. of Succ. Nest</i>	0.4 ± 0.1	0-0.93	0.32**	0.12*	-	-	-
<i>Years Used</i>	7.1 ± 0.2	3-10	0.92**	-0.04	0.30	-	-
<i>Fledged/ Year Used</i>	3.8 ± 0.2	0-8.60	0.53**	0.39**	0.80**	0.46**	-
<i>Fledged/ Year</i>	2.9 ± 0.2	0-8.60	0.79**	0.25*	0.65**	0.76**	0.88**

Measures of productivity were not independent of each other (Table 1). The number of nesting attempts was highly correlated with the number of years used, probability of nest success, number fledged per year and fledged per year used. The fledglings per successful nest was weakly correlated to the probability of nest success but was not significantly correlated with number of nesting attempts or number of years used. Not surprisingly, number of fledglings per year was strongly correlated with number of fledglings per year used as were number of nesting attempts and number of years used. The number of fledglings per year used was associated with the probability of having a



successful nest and to the number of fledglings per successful nest. Number of nesting attempts was most associated with the number of years used and the number of fledglings per year. Nesting attempts will be used extensively throughout the rest of the analysis and will suggest relationships with its associated components.

Table 2. Nested analyses of variance for *F. passerinus* productivity measures at different scales. Fence ( $n=15$ ) is nested within area ( $n=2$ ) and box ( $n=106$ ) is nested within fence.

Productivity Components	Level of Analysis	F-Ratio	<i>P Value</i>
<i>Nesting Attempts</i>	Area	21.51	<0.001
	Fence	12.56	<0.001
	Box	3.25	<0.001
<i>Fledged/ Succ. Nest</i>	Area	0.11	0.74
	Fence	1.62	0.08
	Box	1.01	0.47
<i>Prob. of Succ. Nest</i>	Area	1.41	0.24
	Fence	2.70	0.001
	Box	1.32	0.03
<i>Years Used</i>	Area	6.84	0.01
	Fence	3.88	<0.001
	Box	-	-
<i>Fledged/ Year Used</i>	Area	3.33	0.07
	Fence	2.90	0.001
	Box	-	-
<i>Fledged/ Year</i>	Area	13.69	<0.001
	Fence	9.23	<0.001
	Box	1.93	<0.001

Differences in productivity occurred between mean values of breeding components at the box, fence, and area spatial scale (Table 2). Nesting attempts and the number of fledged per year were both significantly different at all spatial scales. The number of fledglings per successful nest did not differ significantly at any of the spatial scales. The probability of nest success and the number of fledged per year used both did not differ significantly at the area scale but did so at the other scales. The number of years used was significantly different at both the fence and area scale.

**Relationship between Productivity and Habitat at Multiple Scales** To simplify the analyses a principal component analysis (PCA) was used to reduce the data into

comprehensible parts. The PCA reduced the habitat variables into three components for both the neighborhood and microhabitat scale (Table 3). The microhabitat components consisted of a factor characterizing the water and ground vegetation (Water) while one characterized the ground and canopy cover (Canopy) and one final factor characterized vegetation from 1 to 2 meters (HighVeg). The neighborhood component consisted of a food component (Croton), a canopy and high vegetation component (Canopy), and finally a water component (Water).

Table 3. Results of the principal component analysis showing the loadings of the habitat variables within each of the principal components. Loadings greater than 0.5 are shown in bold.

Scale:	<i>Microhabitat</i>			<b>Neighborhood</b>		
	PC1 Water	PC2 Canopy	PC3 HighVeg	PC1 Water	PC2 Croton	PC3 Canopy
<i>Canopy Cover</i>	0.13	<b>0.78</b>	0.32	0.12	0.40	<b>0.75</b>
<i>Water Cover</i>	<b>0.77</b>	-0.43	0.26	<b>0.87</b>	0.30	0.11
<i>Ground Cover</i>	-0.15	<b>0.88</b>	-0.17	<b>0.76</b>	0.34	0.13
<i>Water Depth</i>	<b>0.83</b>	-0.41	0.18	<b>-0.88</b>	0.30	0.12
<i>Veg. Count 0-0.5m</i>	<b>-0.78</b>	-0.19	-0.28	<b>0.64</b>	-0.49	-0.07
<i>Veg. Count 0.5-1m</i>	<b>0.59</b>	0.11	-0.06	-0.48	0.08	0.14
<i>Veg. Count 1-1.5m</i>	0.05	-0.00	<b>0.81</b>	-0.37	0.00	0.43
<i>Veg. Count 1.5-2m</i>	0.20	0.04	<b>0.80</b>	-0.36	0.17	<b>0.61</b>
<i>Croton Stem Count</i>	-	-	-	0.15	<b>-0.91</b>	-0.01
<i>Croton Pod Count</i>	-	-	-	0.16	<b>-0.88</b>	-0.13
<i>Hyptis Stem Count</i>	-	-	-	0.00	-0.12	<b>0.71</b>

The microhabitat components explained very little of the variation in breeding success. Nesting attempts were slightly correlated with Canopy ( $r^2=0.04$ ,  $p=0.05$ ). Water and HighVeg were not correlated with any of the breeding components ( $r^2<0.05$ ,  $p>0.05$ ). Besides nesting attempts, Canopy was also not significantly correlated with anything ( $r^2<0.05$ ,  $p>0.05$ ).

The neighborhood analysis showed a number of different trends however. The analysis of Water was split between the two areas, upland and lowland. Trends were significant in the lowland where more water is located, between Water and fledglings per

year, nesting attempts, and number of years used ( $r^2 > 0.10$ ,  $p < 0.05$ ). No trends were significant in the upland. Croton showed similar trends as Water in that breeding was more successful in areas with low Croton and that fledglings per year and number of nesting attempts were well correlated with it ( $r^2 > 0.10$ ,  $p < 0.05$ ).

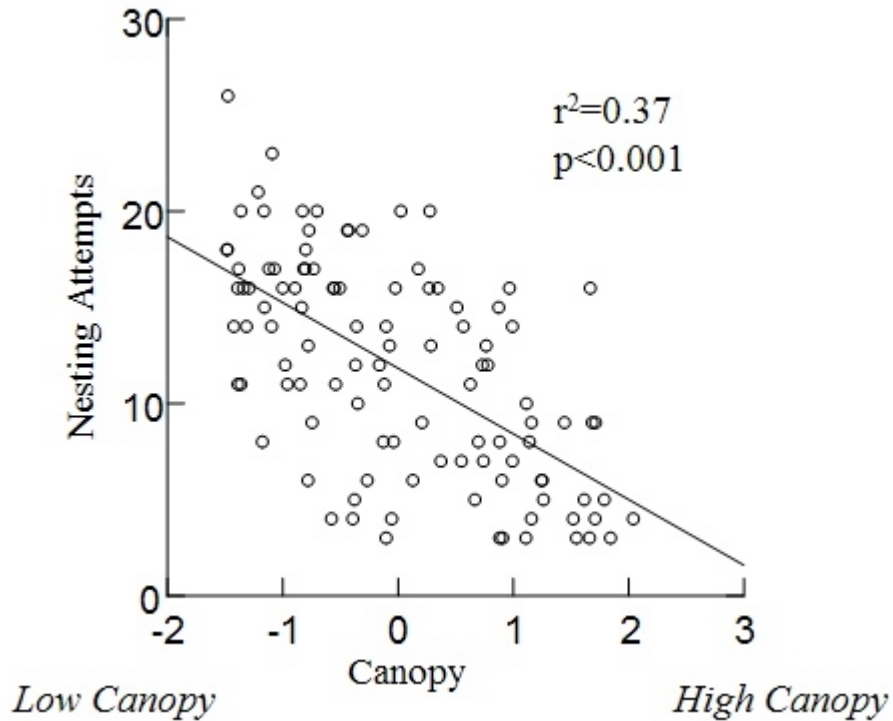


Figure 3. Shows the relationship between the number of nesting attempts and Canopy at the neighborhood scale.

Of the three habitat principal components at the neighborhood scale, Canopy had the greatest effect on the various breeding components. The number of nesting attempts was highly correlated with Canopy independent of the area (fig. 3) as was fledglings per year ( $r^2 = 0.19$ ,  $p < 0.01$ ). The rest of the breeding components were not well correlated with Canopy.

The fence line variation in productivity is also explained well by Canopy. If analysis is split by area then it is clear that much of the lowland fence line variation in nesting attempts is explained by Canopy ( $r^2 = 0.83$ ,  $p = 0.03$ ,  $n = 5$ ). It also explains upland variation well ( $r^2 = 0.58$ ,  $p < 0.01$ ,  $n = 9$ ). Also, fence line variation in fledglings per year is explained well by Canopy (fig. 4) in the lowland. Fledglings per year used is also

explained well in this analysis ( $p=0.03$ ,  $r^2=0.85$ ,  $n=5$ ). Upland variation is not explained well however for either fledgling per year or fledgling per year used ( $r^2<0.10$ ,  $p>0.20$ ,  $n=10$ ). The other breeding components are also not significantly correlated with Canopy at the fence level.

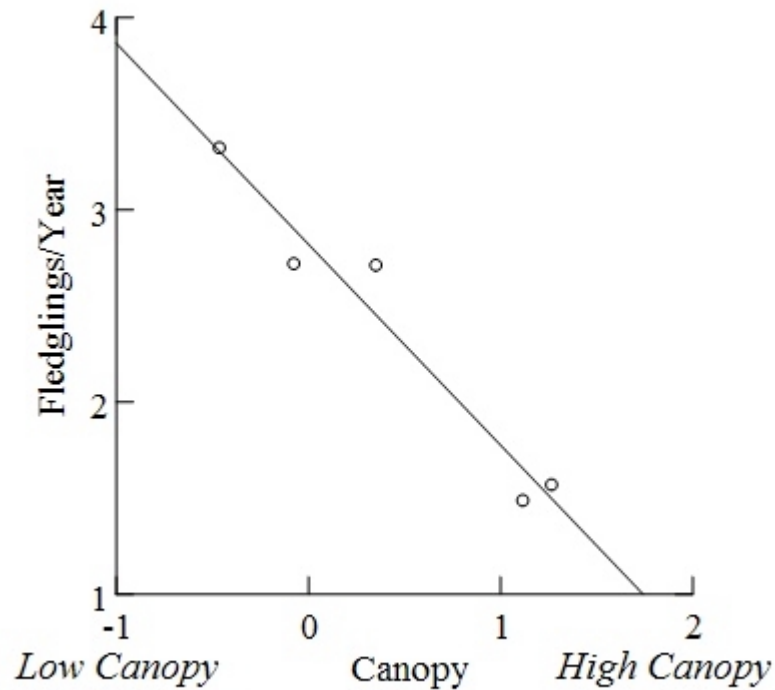


Figure 4. Lowland fence line variation in fledglings per year is explained well by Canopy ( $r^2=0.95$ ,  $p=0.005$ ) at the neighborhood scale.

**Habitat Selection and Nest Mortality** Two types of nest mortality were analyzed in the context of habitat structure; predation and conspecific competition (infanticide/harassment). Predation was analyzed separately within each area (lowland vs. upland) and was found to be significantly correlated with Canopy and Water in the lowland but not in the upland (fig. 5). More predation occurred in areas with less water and more canopy cover.

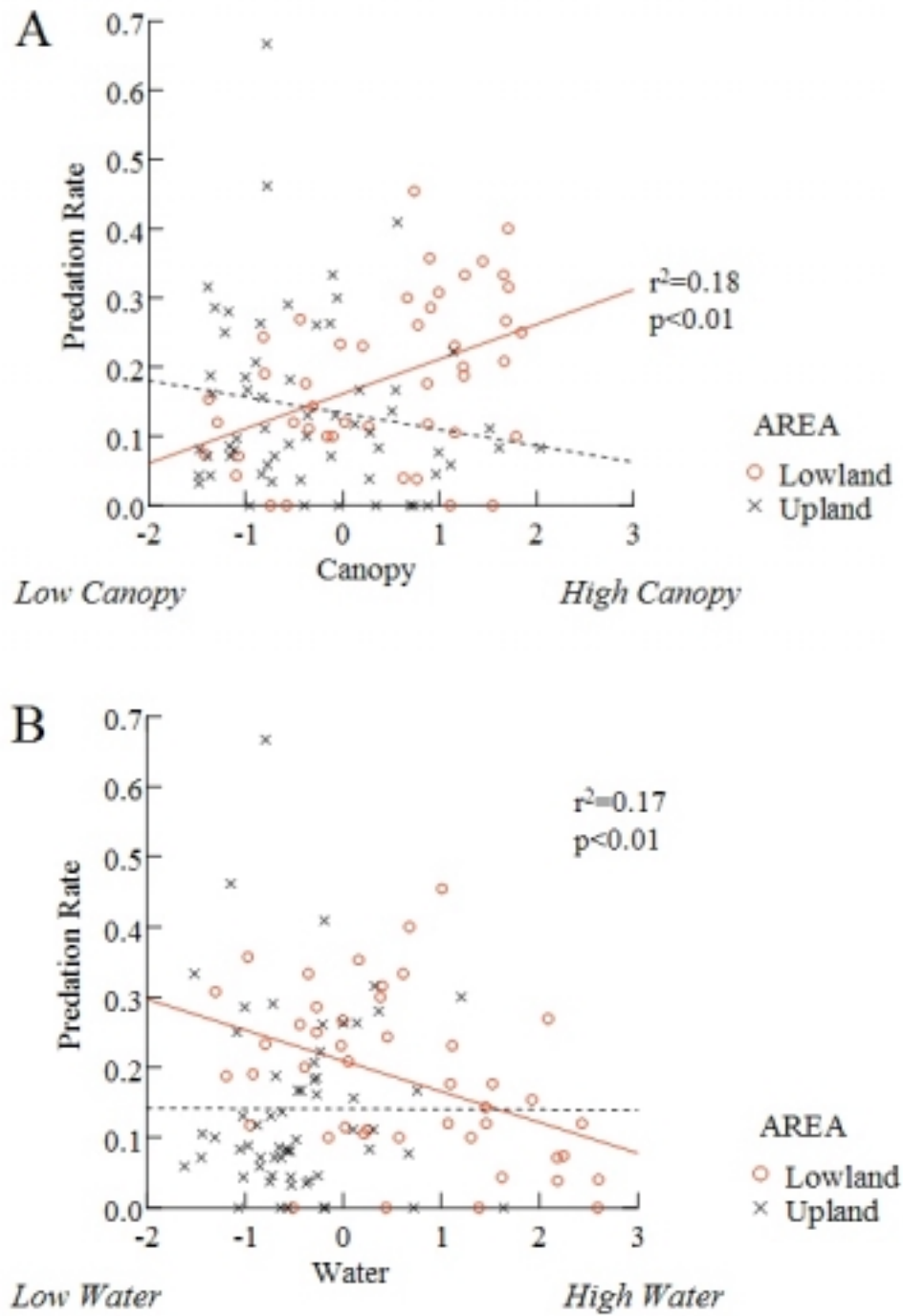


Figure 5. Trends in predation. At the neighborhood scale, 5A shows how predation varies in response to Canopy while 5B shows how predation varies with Water. Note that no significant trends appeared in the upland but did in the lowland.

An opposing trend was seen in nest mortality by conspecifics. Nests in more open areas had a higher chance of nest mortality caused by neighbors or other individuals in the *Forpus* population (fig. 6). Canopy at the neighborhood scale was a significant factor in nest mortality by conspecifics in that boxes with more nest failures (by competition) also have a lower Canopy score (ANOVA;  $r^2=0.10$ ,  $p<0.01$ ). The other habitat components were not related to the probability of mortality by conspecifics ( $p>0.05$ ).

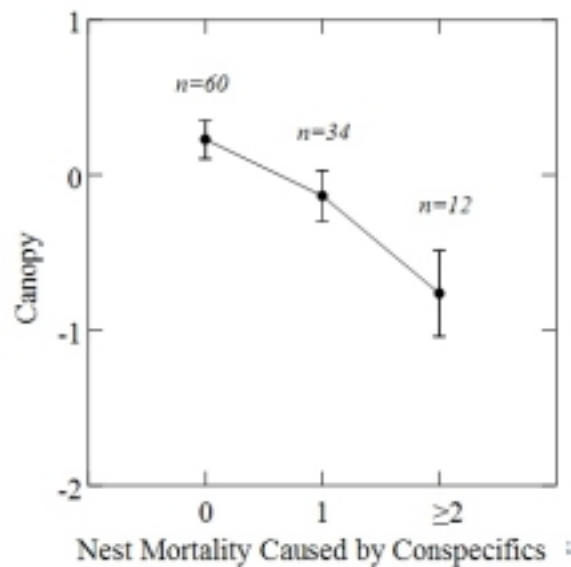


Figure 6. Groups correspond to numbers of nest failures over the ten year period at a given box. The differences in CANOPY between each group is shown.

**Habitat Manipulation** Of the 22 nest boxes, 11 nests were initiated. There was no significant difference between numbers of nests initiated in the experimental boxes ( $n=6$ ) and the control boxes ( $n=5$ ). Of the 11 nests, 8 were depredated and only 3 nests survived to fledge. Again no significant differences were found in predation between the experimental boxes ( $n=4$  or 67%) and the control boxes ( $n=4$  or 80%). Further examination of the depredated nests found that nests in the experimental boxes tended to last longer than nests in the control boxes though the trend was not significant (fig. 7). Also, nests in the experimental boxes tended to be initiated earlier though that trend was also not statistically significant. In fact, 4 experimental pairs had nests in both the control

and experimental boxes and each of these pairs had earlier nest initiation in the experimental boxes.

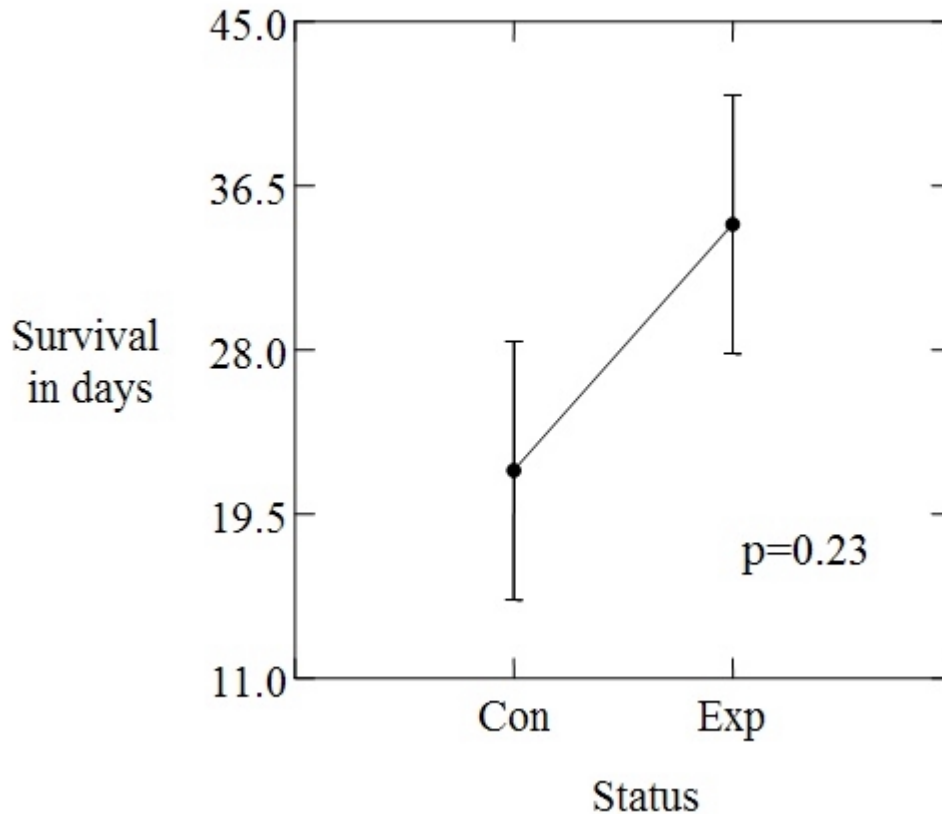


Figure 7. A t-test was performed in order to find differences in survival between the control and experimental boxes. Though the trend was in the direction expected it was not significant.

## Discussion

Breeding success varied over several spatial scales and habitat differences explained much of this variation. *F. passerinus* did not nest often in sites with great amounts of vertical habitat heterogeneity. Also, sites with larger amounts of water at the base of the nest site were preferred over sites without water.

Croton was significantly correlated with fledglings per year but in the opposite direction than we expected. I suspect that food is not important to nest site selection at the neighborhood and microhabitat scale and that this trend can be attributed to the fact

that more food means more vegetation which is less desirable in a nest site as already explained. Perhaps at a larger scale, at the landscape level for example, food would be more important.

The results between the two scales analyzed here were quite different in their explanatory power. While the nesting attempts were correlated with Canopy at both the neighborhood and microhabitat scale, the microhabitat scale only accounted for 3% of the variation while the neighborhood scale accounted for 39%. Additionally, this was the only breeding component that could significantly correlate with the habitat at the microhabitat scale. The nest boxes are all the roughly the same height, size, and shape which could be a controlling factor for nest site selection at this scale. Variation in nest height, size, and shape are likely an important consideration in the analysis of nest site selection at the microhabitat scale but was not examined in this study.

The specific mechanisms that cause the variation in neighborhood habitat selection were also explored and it was found that predation is greater at the less desirable nesting sites (those with less water and greater canopy cover). Martin (1993) suggests that predation is the major force driving nest site selection and certainly this study shows some evidence of this. Most studies of predation in bird nests have attested to the concealment hypothesis (Martin and Roper 1988), that more vegetation around a nest site will hide the nest from predators. This study does not support this hypothesis and instead resembles studies of other grassland species (Winter et al. 2000) in which predation is lower the further it is out in the open. Nests were in artificial nest boxes, which are often not a good indicator of natural nest dynamics (Mezquida and Marone 2003). However, all boxes were placed along fence lines where *F. passerinus* were actually nesting prior to nest box addition (Beissinger and Bucher 1992).

The habitat manipulation experiment provided weak support for predation as a major component to *F. passerinus* nest site selection. Differences in survival between the control and experimental boxes, suggest that open boxes survive longer. However, the sample size of the manipulation experiment was small and all trends found were not significant. To fully understand the mechanism of predation and its effect on nest site selection a more integrated approach is required (Weatherhead and Bloun-Demers 2004) to relate predator densities to nest site habitat features.



Competition for boxes in high quality locations may offset some of the benefit derived in selecting for nest sites in low predation risk areas. Infanticide and conspecific harassment are two important forms of nest mortality and could ultimately be a strong selective force in addition to and in opposition to predation.

Individual variation in quality is also certain to play a role in breeding success and is a subject for future study. Also, further exploration of how scale (temporal and spatial) may affect these patterns would be crucial to complete comprehension of *F. passerinus* nest site selection. An integrated GIS approach to this question of habitat effects could illuminate the larger scale patterns that are potentially driving *F. passerinus* breeding success.

**Conclusion** This research has shown that habitat affects breeding success in *F. passerinus* and that the most successful of nests are located in areas with less vegetative structure and more water. Through correlative evidence we have also shown that predation and social pressure (intraspecific competition) may be the mechanisms creating these patterns. The patterns and processes of *F. passerinus* reproductive success in response to habitat structure have the potential to supplement the conservation of other neotropical parrots, birds, and organisms world wide.

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